The Stratification-Redry Technique with Special Reference to True Fir Seeds

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Abstract-A method of more completely removing seed dormancy and obtaining very rapid and more complete germination of true fir species is reviewed. Detailed use of the method is described, emphasizing standardization and consistency. Tests on other coniferous species are described, and an explanation of how the method works is offered.

INTRODUCTION

Traditionally, seeds of true fir-*Abies* species have been typically poor in quality, germinating erratically and unpredictably, and the bane of nursery growers. Many, if not most, of these problems were related to the phenomenon of seed dormancy, an evolutionary trait that delays germination after natural seedfall until environmental conditions are favorable for seedling growth. Also, until relatively recent times, seed producers tended to process true fir seeds for quantity, rather than for quality. This situation has now changed, especially with the better understanding of seed dormancy, and the development of a method that more completely eliminates this condition. The method is known as the "Stratification-redry technique", and the purpose of this paper is 1) to review the kind of results that can be expected from use of this method on true fir species, including results from nurseries, 2) to describe in detail how the method should be applied, followed by 3) its effects on seeds of other coniferous species, and 4) a brief discussion of how the method works.

1. RESULTS OBTAINED WITH THE STRATIFICATION/RE-DRY METHOD ON TRUE FIR SEEDS

A. The effect of re-drying with further storage/stratification

Briefly, the stratification-redry technique involves partial-redrying of seeds that have already been stratified, then continuing their stratification at a reduced moisture content. This second period of stratification is often referred to-and will be referred to here-as "storage" for simplicity, although it actually is a continuation of stratification.

Grand fir (*Abies grandis*)
When seeds of grand fir were stratified in a fully imbibed state for 4 weeks at 20C, then removed from the refrigerator and dried to three new moisture levels, and stored in the same refrigerator for a further 12 weeks (that is, their stratification was continued for another 12 weeks, but at reduced moisture contents), they germinated in the laboratory as shown in Figure 1.

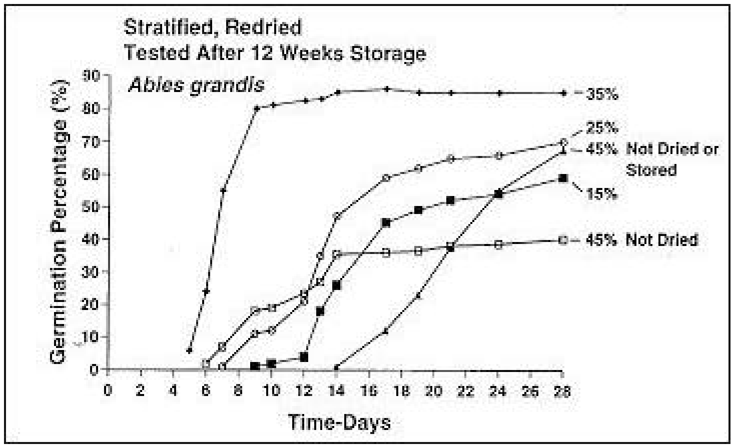

Figure 1. Cumulative germination in stratified grand fir seeds following redrying to four moisture contents and storage for 12 weeks at 20C.

The results show that:
a) Seeds dried to 35% moisture content

- i) began germinating earlier than seeds at any of the other moisture levels,
- ii) germinated most rapidly, reaching 80% less than a week later, and
- iii) maximum germination, 85%, was achieved within 2 weeks. Whereas 15% of these seeds did not germinate, over 94% of all the seeds that did germinate after receiving this combination of treatments had done so within 9 days of being placed in the germinator.

b) Seeds dried to 25% and 15% moisture contents germinated better than seeds that were not dried at all.

c) Seeds not dried from their original 45% moisture content, but that were stored for the additional 12 weeks (i.e. stratified 16 weeks at the full moisture content) began germinating quickly, but had the lowest (40%) germination overall. This was almost entirely attributable to seed deterioration due to microbial activity during the long stratification.

d) As a control, a fifth sample of seeds that had been routinely stratified for 4 weeks with no drying or storage, that is, tested immediately (curve labeled "Not Dried Or Stored") did not begin germinating until day 14, but reached almost 68%, third best overall, by the end of the test. All the seeds referred to in a, b, c and d were germinated simultaneously, in the same germinator; that is, stratification of the last mentioned control sample of seeds began when the other samples had been in storage in the refrigerator (at their adjusted moisture contents) for 8 weeks.

B. The effect of re-drying without additional storage

It is important to distinguish the effect of drying from the effect of additional storage. To do this, samples of the seeds described above were tested for germination immediately after drying without any additional storage (Figure 2).

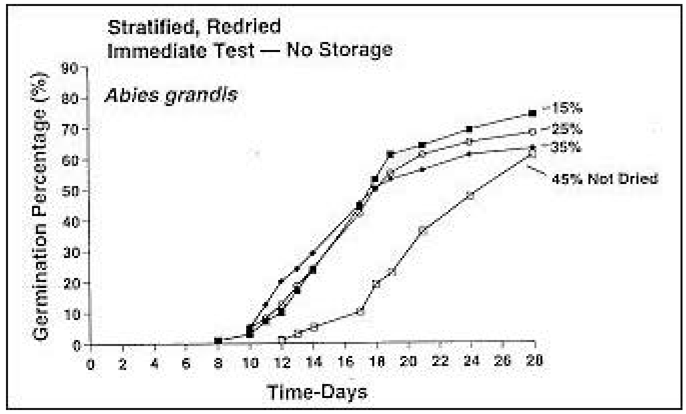

Figure 2. Cumulative germination in stratified grand fir seeds following redrying to four moisture contents - no storage, tested immediately after drying.

These results showed that:

a) drying the seeds to between 15% and 35% had an immediate, major impact on germination speed, but had little effect on final germination capacity.

b) dried seeds germinated 5-6% higher than routinely stratified (not dried) seeds by the mid-point of the test, although the differences in final germination capacity were not so large. Thus, drying alone greatly increased germination speed.

c) Comparing Drying Alone with Drying Plus Storage:
When the germination of seeds that had been dried, but not stored (Figure 2), was compared with the germination of seeds that had been dried and stored for an additional 12 weeks (Figure 1), the difference was mostly on germination speed, although germination capacity (completeness of germination) was increased also. While drying induced some increase in germination, a much larger increase was obtained after the dried seeds had been stored.

d) Comparing the Two Control Samples
The control seeds that were routinely stratified without drying or storing (Figure 1, "Not Dried or Stored"), and that were tested at the same time as those that had been dried and stored (also Figure 1), germinated almost the same as those routinely stratified seeds (Figure 2, "Not Dried) that were tested alongside seeds that were dried, but which were tested immediately without storage (also Figure 2). Whereas the first control seeds were tested three months later than the second, there was only a 4% difference at the mid-point of the test, and a 6% difference at the conclusion. This level of variation was well within expected experimental error, and the shape of the two germination curves were almost identical, indicating that the results were repeatable.

CONCLUSIONS

Three main conclusions were drawn from these data:

i) drying grand fir seeds to between 15% and 35% moisture content (a relatively wide

window) immediately after routine stratification and before they are sown, increased germination speed.
ii) drying stratified grand fir seeds to 35% moisture content, and continuing their stratification at this moisture level in the same refrigerator for another 12 weeks, produced the earliest germinants, yielded 80% germination in 8 days, and complete germination was obtained in 14 days.

iii) prolonging the stratification of grand fir seeds without drying them was detrimental to their quality.

RESULTS WITH OTHER TRUE FIR SPECIES

While the tests described above were being run, other work was carried out on seeds of Pacific silver fir (also known as amabilis fir), and subalpine fir. All of this research has been published (see "Suggested Reading" at the end of this paper), so only a summary is included here.

Pacific silver fir (*Abies amabilis*)

When Pacific silver fir seeds were dried to 35% moisture content and stored for 2, 4 and 12 weeks, germination speed increased to 43.7%, 50.7% and 57.3% respectively, representing increases of 6.5, 7.6 and 8.6 times respectively, over the control. For these same storage periods, germination capacity increased from 37% in routinely stratified seeds (no drying or storage) to 65.7%, 65.3% and 61.3%, respectively, representing increases of approximately 1.7 times over the control. The best overall germination was obtained after 3 months' storage at 35% moisture content when almost 94% of all the seeds that would germinate had done so within the first two weeks of the test. This demonstrated again that, even though germination capacity was increased, the effects were largely on germination speed.

Subalpine fir (*Abies lasiocarpa*)

Routinely stratified seeds (not dried or stored) germinated 10.0% after 14 days and 15.5% after 28 days. When stratified subalpine fir seeds were dried to 35% moisture content and stored for an additional 12 weeks, germination after 14 days reached 69.0%, and after 28 days reached 69.5%, that is germination was almost complete within two weeks. When seeds at 35% moisture content were stored for 6 months germination was complete at 14 days, reaching 73.5%; no more germination occurred during the second part of the test. These finding emphasized, again, that the main effect was on germination speed. Longer storage times were tested, but they did not produce further increases in germination.

RESULTS FROM OTHER TESTS INCLUDING OPERATIONAL NURSERY TRIALS

To find out if drying stratified true fir seeds to 35% moisture content, and then storing them for 3 months, would consistently improve germination, the treatment combination was applied to 30 seedlots of Pacific silver (amabilis) fir. Without fail, all lots germinated faster and more completely than routinely stratified controls (not dried or stored). The increases in final germination ranged from 5% to 45%, and actual germination exceeded 80% In 14 lots, and was 90% or higher in 3 lots. In all 30 lots, germination speed was consistently increased.

The method was applied to over 50 lots more of all three species, grand fir, subalpine fir and Pacific silver fir, as well some noble fir lots, with similar results.

When noble fir seeds from four Washington State seed zones were stratified for 4 weeks, dried to 25% and 35%, and then stored in a refrigerator for an additional 12 weeks, in the laboratory they out-germinated the non-dried controls both in terms of speed and completeness. At 35% moisture 'it was estimated that storage could be extended to 24 weeks after the original stratification, without affecting seed quality. This would be useful in accommodating any delay in sowing.

From nursery tests on the same seedlots, it was estimated that because of improved nursery-bed emergence, plantable seedling yields were increased by 10%- 19% over conventional stratification. Some of the lots showed premature germination in the refrigerator when they were stored for 3 months at 35%, so it was recommended that, for operational purposes, seeds should be redried to around 30% moisture content, which would reduce the tendency for pre-germination without sacrificing any of the beneficial effects on speed of germination and completeness of germination.

In another independent nursery trial on noble fir, a 30-day stratification followed by drying and another 30-day storage gave better results than stratification alone, or longer storage after drying. More than 90% of the seeds that would germinate had done so within the first 2 weeks, and final germination was doubled over the controls.

Nursery tests in British Columbia revealed that the method did not work well on seeds that had been collected early (latter part of August) in the cone-crop season. It was conjectured that these seedlots may not have been mature and, therefore, they were not as dormant. This was based on the relationship observed between seed maturation and dormancy in noble fir, specifically that dormancy increased as the seeds matured. It has long been known that mature seeds (of most tree species) usually fail to respond to stratification; in fact, stratifying immature seeds often reduces germination instead of increasing it. Also, immature seeds often decrease in viability if they are placed in dry, cold storage, and any subsequent stratification may have an adverse effect.

2. HOW TO USE THE STRATIFICATION RE-DRY METHOD

A. The Difference Between Stratification/ Re-Dry and Routine Stratification

The stratification/re-dry method differs from traditional stratification as shown diagramatically in Figure 3.

The upper part of this diagram depicts traditional stratification.

a) In this seeds are: soaked in water for 24-48 hours at room temperature, then
b) drained, and

c) chilled at 20C for 4-8 weeks in their "fully imbibed state" seeds this means that their moisture content is around 45-55% fresh, until

d) they are sown in the nursery.

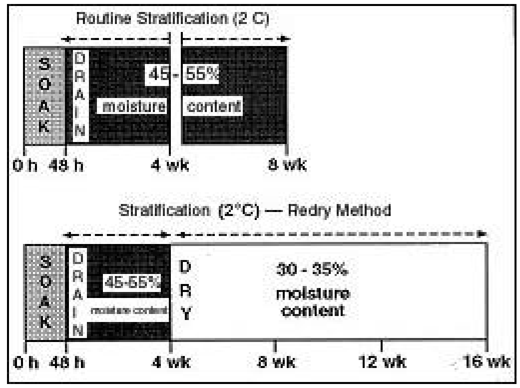

Figure 3. Schematic contrast between the traditional method of stratification (upper) and the new stratification/re-dry method (lower).

The lower part of Figure 3 shows the stratification redry method. In this seeds are:

a) soaked for up to 48 hours at room temperature (as in the old method),

b) drained (as in the old method), then

c) chilled for 4 weeks while fully imbibed (as in the old method). After 4 weeks of chilling, the stratified seeds are removed from the refrigerator and

d) dried until their moisture content is 30-35%, then

e) returned to the refrigerator for an additional 4-12 weeks, until

f) they are sown in the nursery

The two methods are identical through steps a), b) and c), but the newer method adds two more steps, d) and e), before the seeds are sown.

B. How the Stratification/Re-Dry Method Is Applied

STEP 1. Soak the seeds in tap water for 48 hours. "2 days" is sufficient, but some consistency should be applied. If the seeds are put in water around mid-day, and removed first thing in the morning two days later, this will be adequate, but the operator should aim to follow the same process with each subsequent seedlot. This moisture is required to re-hydrate seed tissues that may have been dried to a moisture content of below 10% for cold-storage, and allows the biochemical changes to begin that correspond with a removal of seed dormancy. Hydrated seeds respire, even under water, so good aeration is required.

STEP 2. Remove the seeds from the soak water and drain them thoroughly, but do not permit them to dry out other than a slight surface drying, at this stage.

STEP 3a. Place the hydrated seeds into the container-plastic bag or whatever-in which they are to be chilled. All containers should be large enough that a volume of air several times the volume of the seeds is enclosed. Bags may be suspended in the refrigerator, and the bottoms punctured so that free water can escape. Bags are often loosely tied, or a "breather" tube is placed in the neck, so that there is a channel for air exchange, but not so much that the seeds are going to lose moisture.

Hydrated seeds respire, even at chilling temperatures, so good aeration is required:

(a) to prevent carbon dioxide build up,

(b) to ensure they are adequately supplied with oxygen, as well as

(c) to minimize heat accumulation from respiration. Some operators also lightly "massage" the bags once or twice each week to move the seeds around so that conditions within the seed mass stay as uniform as possible.

STEP 3b. Stratify the seeds. Place the seeds in a refrigerator so that they achieve and maintain a temperature of between 1^o and 3^oC. This temperature, often stated as 2^oC, is critical as it favors the biochemical changes and morphological developments that lead to rapid and complete germination when the seeds are sown. Low temperature also reduces decay caused by microorganisms. Many manuals prescribe 5^oC, but if the refrigeration unit is used for other purposes, and it is opened frequently, seed temperatures many not remain as low as 5^o for the full duration. It has been shown that:

a) temperatures above 5^oC are far less effective for stratifying tree seeds, and

b) any less-dormant seeds in the bag are likely to chit (begin germinating) at the higher temperatures, rendering them useless for sowing.

In the wild, the seeds of some coniferous species, including the true firs, are known to germinate in melting snowbanks. Freezing and subfreezing temperatures are not effective in stratification either.

STEP 3c. Stratify the seeds for 4 weeks. This usually means 28 days, or 4 working weeks, but 30 days (1 month) can be tolerated. Longer periods simply delay the next steps, and it is these steps that bring about the improvements in germination.

STEP 4a. Dry the stratified seeds. Remove the chilled seeds from the refrigerator, and adjust their moisture content to 30-35%.

Initial water uptake is regulated only by the time of soaking, and may reach levels of between 45% and 60%, depending on the species and the seedlot, by the time the seeds are placed into the refrigerator. This moisture level must now be reduced to between 30% and 35% of the fresh weight of the seeds.

The procedure for this, which is the most critical step in the entire process, is expressed in Table 1. Although complicated looking, it relies on the simple process of monitoring the weight of the stratified seeds as they dry out.

Table 1. Oven-Drying Procedure

1. a) Take 8-10 samples (more if there is time) of 50 seeds each.

   b) Oven dry (24 hours at 103-105°C) to constant weight.

   c) Cool in a dessicator (minimum 45 minutes to 1 hour).

   d) Weigh.

2. Calculate the average dry weight for 50 seeds.

3. a) Use the average dry weight (item 2) to calculate the new fresh weight at the specified target moisture content (M.C.%) applying the following formulae.

   b) **Formula 1:** Since $\text{M.C.\%} = \dfrac{\text{Fresh weight (FW) - Dry weight (DW)}}{\text{Fresh weight (FW)}} \times 100$

   c) **Formula 2:** Then the $\text{New FW} = \dfrac{\text{Average DW [from step 2]} \times 100}{100 - \text{the specified target M.C.\%}}$

4. a) For example, suppose original FW = 50g, and DW = 40g. The original M.C.% would be calculated as follows:

   $$\text{M.C.\%} = \frac{50-40}{50} \times 100 = \frac{10}{50} \times 100 = 20 \text{ (Formula 1)}$$

   b) So the original moisture content was 20%.

   c) What must the FW be for M.C.% = 15 ?

   $$\text{New FW} = \frac{40 \times 100}{100-15} = \frac{4000}{85} = 47.1 \text{ (Formula 2)}$$

   d) Thus, the new FW must be 47.1 g. That is, the sample must be dried from its original fresh weight of 50g to 47.l g

   e) As a check, use new FW in Formula 1 and calculate the M.C.%, thus:

   $$\text{M.C.\%} = \frac{\text{FW-DW}}{\text{FW}} \times 100 = \frac{47.1 - 40}{47.1} \times 100 = 15.07\%$$

Thus, the actual new moisture content is 15.07%, which is close enough.

5. a) After stratification, air-dry the seeds uniformly, turning them frequently.

   b) Take five or six 50-seed samples to monitor drying. More samples would improve accuracy, but the work must be done quickly and five or six will suffice.

   c) Weigh these samples, and turn main seed mass, every 30 minutes to begin with, then more often as the target moisture content is approached.

   d) The SAME 50-seed samples must be weighed each time, so having weighed the samples once, they must be put back beside the main mass of seeds so that they are subjected to the same drying environment, and so that they can be identified for the next weighing, but they must NOT BE MIXED with the main seed mass.

   e) After each weighing, calculate the average FW for the five (or six) samples.

   f) When the average FW for the five or six samples equals the calculated new FW, stop weighing and quickly re-bag the entire seed mass, including the samples.

6. Re-bag the seeds using dry plastic bags and return to the refrigerator in which the seeds had been originally stratified (2°C).

7. Store the redried seeds in the refrigerator for the specified period, then sow.

Step 4b. Adjusting Seed moisture content to 30-35%

The method uses the average oven dry weight of a given number of seeds. Several samples are necessary, and 50 seeds/ sample is satisfactory if the seedlot is well mixed, but a larger number of seeds per sample may be better if the seedlot is not homogenous. Since the determination is destructive of the seeds, a smaller number of seeds is more desirable. The procedure must be followed for each and every seedlot to which stratification/redry is to be applied.

This determnation is performed on seeds taken from the original storage container, i.e. seeds that have not been stratified. If the entire seedlot is to be stratified/redried and then sown, 500 seeds (10 samples of 50 should be set aside for the dry weight determination.

A. How to determine seed dry weight, and moisture content (optional).
a) Basic oven-drying procedure. Remove several randomly-obtained samples from the seedlot. Dry them in an oven set at 103-105ºC until they reach constant weight, then reweigh. Most manuals and seed testing rule books prescribe that the seeds shall be dried at 103ºC for 17 hours. i) The temperature is critical; it has to be above 100ºC to drive off all the moisture, but not so high as to drive off other chemicals from the seeds so that the overall weight loss represents more than just a loss of water. ii) The seeds must be dried until they stop losing water, i.e. losing weight, and usually a drying period of 17 hours is prescribed for laboratory testing. For operational convenience this period can be extended to 24 hours, so if the drying starts at noon, it should stop at noon the next day. Longer periods and higher (or lower) temperatures must be avoided. Operators should be consistent with their method. iii) It is essential that the hot seeds, and the containers in which they have been dried, be placed immediately in a dessicator until they are cool enough (minimum 45 minutes) to weigh.

2. How to adjust the moisture content to 30-35%
When the average dry weight of 50 seeds has been obtained, the average fresh weight of 50 seeds at a moisture content of 30-35% can be calculated using Formula 2 (Table 1). In Formula 2, which is simply Formula 1 transposed, the average dry weight of 50 seeds is entered, as is the specified moisture content, 30% to 35%. Since this is a range of moisture content two calculations are required, one for the new fresh weight of 50 seeds at 30%, and a second for 35% moisture.

An example of how this works is given in items 4a-e. Samples of stratified seeds have been weighed and the average fresh weight (FW) is 50 g. After drying, the average dry weight (DW) was 40g. Using Formula 1, the moisture content was 20%. What will be the fresh weight if the moisture content is adjusted to 15%? Using Formula 2 it can be calculated that when the fresh weight of a 50-seed sample is reduced to 47.1 g, the moisture content will be 15%.

As a check, (item 4e), the new fresh weight (47.1 g) is entered into Formula 1, along with the average dry weight expression (40g). This gives a moisture content of 15.07% which is well within the tolerances required by the overall procedure.

Thus, the redrying procedure depends on monitoring the changes in fresh weight (FW) of the stratified seeds after they have been removed from the refrigerator. Samples similar to those used to obtain the average dry weight (DW) are used to monitor the change in fresh weight (FW). No oven-drying is needed.

3. The drying operation
To dry the stratified seeds to their new moisture content, they must be spread out in a single-

seed layer, preferably on an absorbent material. Newspaper works well for this, as well as making seed handling relatively easy when rebagging. Five to six samples of 50 seeds, at random spots among the spread seeds, are counted out. These samples must be clearly delineated from the seed mass, but kept within the seed mass.

The samples are repeatedly weighed until the average of their fresh weights reaches the calculated target fresh weight. The same samples of 50 seeds must be weighed each time, and they must not be mixed into the main seed mass until the drying step is complete. Provided all the seeds, the samples as well as the seed mass, have been dried uniformly, when the average fresh weight of the samples reaches the calculated fresh weight for a moisture content of 35%, preparations should be in hand to rebag the seeds. However, drying can be allowed to continue until the new fresh weight approaches that calculated for a moisture content of 30%. Just before the fresh weight for 30% is reached, all the seeds can be placed in a fresh, dry bag (or bags), and returned to the refrigerator.

Frequent stirring of the seed mass is essential to promote uniform drying; the samples will be adequately "stirred" when they are weighed. Weighings should be repeated every 30 minutes or so to begin with, then, as the target moisture content is approached, at shorter intervals. This is the main reason for using only five or six samples at this stage; the final weighings must be done quickly, more samples might take too much time, and the operator may overshoot the target moisture content.

A range of two moisture contents, corresponding with two fresh weights, is used because i) uniform drying of the main seed mass is difficult and, unless the seeds are truly spread in a single-seed layer and adequately stirred, some may not dry as well as others. Thus, ii) some seeds may still be above 35% when they are bagged, and the less-dormant ones may chit before they can be sown. Especially for large lots, it is recommended that the seeds should be rebagged when the moisture content of the monitor samples is lower than 35%, but above 30%. Based on experience with noble fir seeds, even at 30% the effect on germination speed and completeness will not be seriously compromised. In other words, if an error is made, it is safer to err on the side of dryness than on the side or wetness.

The time to dry the seedlot to a moisture content of 30-35% depends on how wet the seeds are to begin with, what the ambient conditions - air temperature and humidity are during drying and, to a certain extent, how frequently the seeds are stirred. A warm room can be used, especially if outside conditions are cold and moist, but the seeds should not be oven-dried. A circulating fan blowing air across the seeds greatly speeds up the drying process. Under favorable conditions, seeds will reach their new moisture level within 3-4 hours.

To verify that the moisture content achieved is the correct one, at least 4 small samples (about the same size as 50 seeds, but not necessarily counted out), should be removed and quickly weighed to get fresh weights, then dried for 24 hours at 103-105°C, cooled in a desiccator, and re-weighed. The average fresh and dry weights for these samples are then used in Formula 1 to determine the real moisture content. Experimentally, it was found that the method described above gave target moisture levels within +2.5%, which is accurate enough for operational needs.

It must be emphasized that when stratified seeds are to be dried as part of the procedure described here, they are done so at ambient air temperatures, that is, at a room temperature no higher than 23-25°C, or even at external air temperatures that are typically below 20°C. At no times are the seeds dried at elevated temperatures, that is, in an oven; oven-drying is used only when moisture contents are to determined. Throughout the method, moisture contents are expressed as a percentage of the fresh, or starting, weight of the sample. Fresh weight moisture content is the international protocol for expressing seed moisture contents, and it differs from the more-accepted scientific protocol of expressing moisture contents on the dry, or final, weight of the samples. Thus, if the label on a 100 kg bag of seeds declares that the moisture content is 6.7%, the prospective buyer knows immediately that there are 6.7 kg of water in the seed mass. If the moisture content was expressed "scientifically", in this example it would be 7.2%, which is less easily calculated.

3. USE OF THE STRATIFICATION/REDRY METHOD ON SEEDS OF OTHER SPECIES

The stratification/redry method was tested in the laboratory on a small scale on seeds of five other coniferous species, western hemlock, white spruce, lodgepole pine, Douglas-fir and Sitka spruce. All the seeds were routinely stratified for 4 weeks. They were then redried to four moisture levels, including no drying (the normal moisture content at the end of stratification); for western hemlock, lodgepole pine, and Sitka spruce, the new moisture levels were 25%, 20% and 15%, for Douglas-fir 35%, 25% and 15% were tested, while for white spruce 30%, 22.5% and 15% were compared.

a). Western hemlock (*Tsuga heterophylla*). Germination capacity tended to decrease in dried seeds, especially with longer storage, but no statistically significant effects were found. Germination speed was significantly reduced at 15% moisture content following 2 or more weeks of storage. Germination speed was significantly increased in seeds stored for an extra 4 weeks without any redrying, that is, a total of 8 weeks of stratification, confirming earlier research on stratifying this species

b). Lodgepole pine (*Pinus conforta*). Germination speed was significantly increased when seeds were stored for 2 to 12 weeks without redrying (extended stratification). Fastest germination occurred in seeds stored at 25% moisture content for 12 weeks. Germination speed was significantly reduced in seeds dried to 15% moisture content and stored for 2 or 4 weeks. Germination capacity was not affected.

c). Sitka spruce (*Picea sitchensis*). Germination speed was significantly increased in seeds stored for 12 weeks either without drying (extended stratification) or after drying to 25% moisture content. Germination capacity was not affected. Germination speed tended to be reduced in seeds dried to 15% moisture content and stored, but a significant decrease occurred only after storage for 12 weeks.

d). Douglas-fir (*Pseudotsuga menziessii*). Germination capacity in a high quality seedlot (96.5% germination after routine stratification) was unaffected by drying and storage, but redrying, even to 15%, increased germination speed. Fastest germination speed occurred in seeds stored at 35% moisture content for 3 months.

e). White spruce (*Picea glauca*). Germination capacity and germination speed decreased in seeds stored without redrying, although the effect only became statistically significant for seeds stored for 3 months. Germination speed was significantly increased in seeds redried to 30% and 22.5% moisture contents and stored for 3 months. Germination was slower in seeds stored at 15% moisture content.

These results suggest that the stratification/redry procedure may not be a panacea for all species, but the moisture levels tested probably were not the ideal ones for these species. However, statistically significant gains in germination speed were obtained in Douglas fir, the two spruces and lodgepole pine. The seedlots used were already of relatively-high quality (over 80% germination capacity), so not much improvement in germination capacity could have been expected. The results showed that any level of drying, even without further storage, was detrimental to western hemlock.

4. HOW DOES THE STRATIFICATION/REDRY METHOD WORK?

The increases in germination speed are brought about mainly by a synchronization of the germination of individual seeds. Less-dormant seeds that are predisposed to germinate rapidly are prevented from doing so by the moisture stress imposed at the reduced moisture content, a moisture stress that is not so great as to prevent the occurrence of the processes that accompany dormancy removal. This phenomenon is similar to the so-called "priming" and "conditioning" effects that have been reported when seeds were treated with osmotic solutions such as polyethylene glycol (PEG).

By returning the seeds to cold storage after redrying, the more dormant seeds are allowed to "catch up" in terms of dormancy removal, and at the reduced moisture content it appears that dormancy removal may be more complete. When the seeds are freed from the moisture stress by being given a free water supply in a favorable environment (when they are sown), all the seeds that can germinate do so synchronously. This is believed to be the reason why, for stratified grand fir seeds redried to 35% moisture content and stored for 12 weeks (Fig. 1), the germination curve was so steep during the first 10- 12 days, after which it abruptly leveled off. ne seeds that did not germinate were dead.

The benefits of controlling seed moisture contents during stratification have not been confined to coniferous seeds. Research on ash (*Fraxinus*) and beech (*Fagus*) seeds has found similar responses. In France, it was shown that freshly-collected beech nuts can be stratified at 30% moisture content, then air-dried to 8% moisture and stored at below freezing temperatures for at least 3.5 years. When re-hydrated, germination in this species is complete and rapid. The initial moisture level for stratification is the same moisture level that works with true fir seeds. This evidence suggests that the phenomenon may be found in a wider variety of tree seeds.

Interest in the stratification/redry method has been shown in Europe, especially in Denmark where there is a large Christmas tree industry based on sowing Nordmann fir (*Abies nordmanniana*) seeds. The Forest Tree Seed Committee of the International Seed Testing Association is studying the introduction of the method into the International Rules for Testing Seeds. Thus it appears that the method is widely recognized, especially wherever true fir regeneration stock is grown.

Moisture management in forest tree seeds may not be a universal solution to complete removal of dormancy in all species, but it appears to have a broadly-based relevance that was largely overlooked until about 15 years ago. More research is needed to determine how other species, coniferous and broadleaved, can benefit from this approach, and to refine the techniques for full-scale, practical application. This will involve testing various moisture levels on numerous seedlots within all species of interest. The moisture content "window" that is effective for true fir seeds is quite narrow, and its achievement is based on closely following the experimental procedure that has been described. A similar approach should be taken when studying other species so that the optimum moisture content can be accurately pin-pointed.

Even though it was not found to work with true fir seeds. one approach that should be investigated is to control the amount of water that the seeds are initially allowed to absorb. Experiments on grand fir and Pacific silver fir curtailed the initial water uptake when seed moisture content had reached 35%. The seeds were then stratified for 1, 2, 3 and 4 months and then tested. Germination never reached the level of routinely stratified seeds suggesting that the initial moisture content had to be above 35% for the initiation of stratification to be effective.

The reason for this is not known, but it may be connected to the pattern of moisture distribution within the seed tissues. Hydrating true fir seeds to 35% takes less time than to full imbibition (45+ %) and, at the time hydration is terminated and the seeds are placed in the refrigerator, the moisture taken up is localized in the seedcoat and outer portion of the megagametophyte (endosperm). Even after soaking the seeds for 48 hours the embryo will not be fully hydrated. In the refrigerator, translocation of moisture to the embryo will proceed at a much slower pace (than at higher temperature) and it maybe that, when hydrated to 35%, there simply was insufficient moisture for the changes to occur that accompany dormancy removal. However, seeds of other coniferous species, and those of broadleaved trees, may behave differently.

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